Prehistoric versus modern Baltic Sea cod fisheries: selectivity across the millennia

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Combining Stone Age and modern data provides unique insights for management, extending beyond contemporary problems and shifting baselines. Using fish chronometric parts, we compared demographic characteristics of exploited cod populations from the Neolithic Period (4500 BP) to the modern highly exploited fishery in the central Baltic Sea. We found that Neolithic cod were larger (mean 56.4 cm, 95% confidence interval (CI) ± 0.9) than modern fish (weighted mean length in catch $= 49.5 \pm 0.2$ cm in 1995, 48.2 ± 0.2 cm in 2003), and older (mean ages $= 4.7 \pm 0.11$, 3.1 ± 0.02 and 3.6 ± 0.02 years for Neolithic, 1995, and 2003 fisheries, respectively). Fishery-independent surveys in 1995 and 2003 show that mean sizes in the stock are 16–17 cm smaller than reflected in the fishery, and mean ages approximately 1–1.5 years younger. Modelled von Bertalanffy growth and back-calculated lengths indicated that Neolithic cod grew to smaller asymptotic lengths, but were larger at younger ages, implying rapid early growth. Very small Neolithic cod were absent and large individuals were rare as in modern times. This could be owing to selective harvests, the absence of small and large fish in the area or a combination. Comparing modern and prehistoric times, fishery selection is evident, but apparently not as great as in the North Atlantic proper.

Keywords: Baltic Sea cod; Neolithic fishery; otoliths; fishery selection

1. INTRODUCTION

Recent documentation of rapid worldwide declines in exploited fish populations (e.g. Botsford *et al.* 1997; Pauly *et al.* 1998; Myers & Worm 2004) has precipitated efforts to understand the root causes, and to piece together more evidence of past conditions against which to measure the current change. Among these, the 'shifting baseline' (Pauly 1995; Pauly & Maclean 2003) of managers and fishers alike, i.e. that the state of a fishery first experienced by a person determines that 'the norm', has led to vast erosion of fishery resources as generations lose track of past abundance. The specific mechanisms vary from place to place, but a general widespread pattern of serial depletions of one stock after another has left a legacy of depauperate marine food webs (Jackson *et al.* 2001; Pauly & Maclean 2003). Thus, there is a strong need to identify past baselines and use these to guide fisheries management, restoration and conservation policy.

Atlantic cod (*Gadus morhua*) ranks, with sturgeon, eels and a few others, as a species having some of the most dramatic of fishery-driven collapses, at least in its western range (Hutchings & Myers 1994; Hannesson 1996; Boreman *et al.* 1997). Northwestern stocks ('northern cod') are so low that recovery of some may be in doubt (Bundy & Fanning 2005). Eastern Atlantic stocks are also in severe decline in the North, Skagerrak and Baltic Seas

(ICES 2007), with such low spawning stock biomasses, poor recruitment and lack of signs of recovery that commercial extinction of some stocks appears to be a real possibility (Jonzén *et al.* 2001).

With cod populations at historic lows and challenges to rebuild them mounting, it is important to explore the past for clues about characteristics such as stock sizes, exploitation rates, age and size structure, etc. and what ecological roles cod would have played when their populations were larger. For example, based on nineteenth century New England fishing logs and other historical data, Canadian Scotian Shelf cod biomass was estimated at 1.26 million metric tonnes (mt) in 1852, compared with only 50 000 mt today (Rosenberg *et al.* 2005). At a longer time scale, comparisons of archaeological and modern data have documented declines in mean length of Gulf of Maine cod from over one metre 5000 years ago to less than 40 cm in the 1980s (Jackson *et al.* 2001). In Europe, North Sea cod fished in medieval times often exceeded one metre (Barrett *et al.* 1999). Recent efforts to synthesize historical accounts over the past 500 years (MacKenzie *et al.* 2002*a,b*) led researchers to conclude that data are at present too sparse to draw a clear picture of causes of change in Baltic Sea cod, but it is apparent that fish populations there have been subject to abiotic (climate forcing, eutrophication) and ecological (predation by humans and marine mammals) pressures for millennia. In the twentieth century, record catches in the early 1980s were due to strong year classes of eastern Baltic Sea cod in 1976, 1977 and 1980 (ICES 2007), reaching peak spawning stock biomass (SSB) of approximately
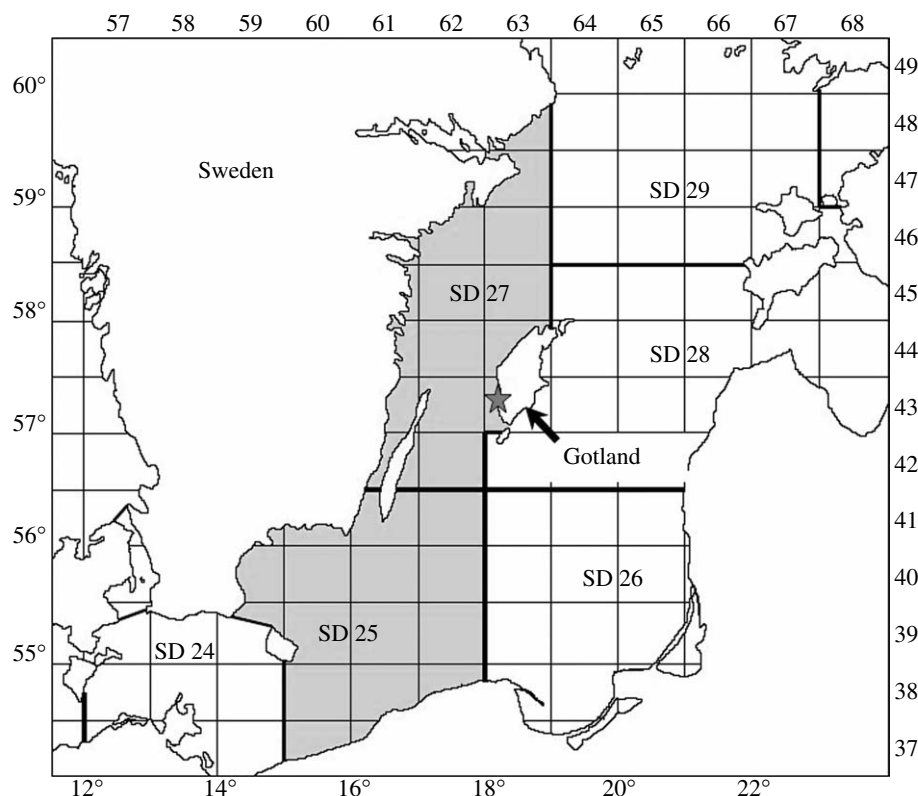
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Figure 1. Location of Ajvide on southwestern Gotland (star). Shaded areas of the Baltic Sea (s.d. 25 and 27) are ICES areas from which 1995 and 2003 samples were drawn.

650 000 mt in the early 1980s. Recent SSB fluctuates approximately 85–100 thousand mt, with variability driven by fishing intensity (Jonzén *et al.* 2001; ICES 2007).

We report here on a novel study that compares characteristics of exploited Baltic Sea cod from two time periods, the Neolithic Stone Age (4500 BP) and recent times (1995 and 2003), from the same general region of the Baltic proper. The year 1995 represents the highest biomass estimates from the past 15 years, and 2003 one of the all-time lows (ICES 2007). Although the archaeological material spans an unknown period of years, we assume that the stocks were more or less in steady state at the time. Thus, characteristics of the stock 4500 years ago may serve as a baseline against which to compare today's situation, in which fishing plays a major structuring role on the Baltic cod stocks. Following the results reported by Jackson *et al.* (2001) and Rosenberg *et al.* (2005), we hypothesized that the characteristics of Stone Age cod populations—presumably less heavily exploited by humans—would be very different from those today. Specifically, we hypothesized that evidence of larger, long-lived fishes would be found.

This comparative study is possible owing to excellent preservation at a site on the island of Gotland, Sweden (figure 1). The site, Ajvide, contains remains from people of the Neolithic Pitted Ware culture (Burenhult 2002). The site has yielded an extensive assemblage of faunal remains, including those of cod captured and eaten. Hundreds of cod otoliths and vertebrae have been recovered, many of them in good to excellent condition (figure S-1 of the electronic supplementary material). Otoliths (earstones) grow incrementally and are known to be the most reliable chronometric structures in fish skeletons (Campana & Thorrold 2001); they are routinely

used today to age most marine teleosts. If validated, analysis of otolith increments can be used to estimate size at capture, age and size-at-age. Similarly, size at capture can be estimated from vertebrae. Population-level statistics can then be developed, such as estimates of mortality rates, average individual growth rates, and changes in size-at-age that might indicate responses to fishing pressure. Although Baltic Sea cod otoliths are not as easy to interpret as those from Atlantic populations, one of us (Y.W.) routinely reads these otoliths for the Swedish Baltic cod stock assessments; thus, any biases will be equally spread among modern and Stone Age samples. Following the analyses, we discuss plausible reasons for the patterns observed.

2. MATERIAL AND METHODS

(a) *Study area*

Neolithic cod remains were excavated at Ajvide, Gotland (57° 16′ North, 18° 7′ East, figure 1). The site is currently 1 km from the shore, but at the time of settlement it was located on a spit of land on the shore of a wide bay that extended into the Baltic (Burenhult 2002). The total site area is approximately 20 ha and today located at 12 m.a.s.l. The main period of occupation was during the Middle Neolithic, 3100–2700 BC and, at *ca* 2900 BC, a (recorded) transgression submerged the area for some time (Burenhult 1997*a*,*b*).

The Ajvide site is excavated for research purposes only, and new areas have been opened up every summer season since 1983. Information from earlier excavation periods facilitated our selection of areas, focusing on those that were especially rich in fish remains.

Modern cod otoliths were selected from fishing areas near Gotland (ICES areas s.d. 25 and 27, figure 1). The routine samples used for ageing are taken from gillnet

and trawl fisheries with the assumption that the gear are length selective, but not age selective. Growth patterns are assumed to be uniform within the eastern Baltic stock, and ageing of cod is pooled within the s.d. 25–32 regions for assessment purposes.

(b) Otolith preparation and measurements

For the modern fishes, stratified samples (at least 10 per 10 cm length class) of sagittal otoliths were randomly drawn from archival collections made from the 1995 and 2003 Swedish national data sampling programme designed for annual stock assessments (Working Group of Baltic Fish Stock Assessment: ICES 2007)[1]. Neolithic fish sagittal otoliths were excavated from different parts of the D-upper and D-lower area (layers 2–4, covering a time span of 200–400 years), cleaned and stored with location information. Prehistoric otoliths selected for analysis were intact and did not have a 'mate' in the same find context, thus assuring that only one otolith per cod was analysed. Totals of 146, 184 and 154 otoliths were read for the Neolithic, 1995 and 2003 collections, respectively.

Otoliths were sectioned to expose the core, ground and polished, and photographed. The reader conducted the age determinations from the photographs, measuring the widths of the annual rings (annuli). Age estimation and measurements were conducted twice (modern material) or three times (Stone Age material). Five Neolithic otoliths were rejected based on damage of the edge (oxidation or breakage) or the lack of examinable annuli. All modern otoliths were readable.

Neolithic cod lengths (cm) at capture were estimated from a regression equation (Olson *et al.* 2002) derived from modern Baltic Sea cod and their otoliths

length at capture

$$= 9.73 \, (\text{otolith maximum width, mm}) - 13.34, \qquad (2.1)$$

$r^2 = 0.92$.

Back-calculated lengths at age were estimated using the equation (Smedstad & Holm 1996)

$$L_i = \left(\frac{O_i}{O_c}\right)^{\nu} L_c, \qquad (2.2)$$

where L_i is length (cm) corresponding to the ith increment; L_c is length at capture; O_i is otolith width (mm) corresponding to L_i; O_c is otolith width at capture; and ν is slope of the regression of LN(L) on LN(O) $= 1.3285$ (from our data). Smedstad & Holm (1996) tested six back-calculation methods on tagged (known-age) fish, and found this method ('nonlinear body proportional') to be the least biased. Length estimates of an individual Neolithic fish varied 0.12–9.5% (mean 3%).

We estimated the season of capture of the Neolithic fish by examining the opacity of the outermost growth zone. Slower growth in cod that would be expected in winter creates more translucent growth zones in their otoliths (Hüssy *et al.* 2004). Growth of the translucent zone would be finished in most individuals sometime between December and March in s.d. 25 (Mosegaard *et al.* 1997). This is also supported by personal experience from routine ageing of Baltic cod.

Size at capture was estimated for an additional 84 otoliths and 269 vertebrae (see Olson & Walther 2007 for details of vertebral measurement). Fourteen vertebrae from fish 70 cm or above were included in parametrization of the von Bertalanffy growth model (see the electronic supplementary material). The remaining 339 fish were aged with the

derived von Bertalanffy growth parameters. Thus, our expanded Neolithic set of observations totalled 520. Note that these individuals were not used for inter-annual growth rate analyses.

Because modern fish length data were reported as frequencies, we calculated weighted mean cod lengths from 1995 and 2003 with data from fisheries (both trawl and gillnet) and fishery-independent surveys ('Argos' trawls; Swedish National Fisheries Board, unpublished data). Ages were estimated by developing an age–length key and multiplying by the observed length frequencies. Mean lengths and ages were calculated for the Neolithic cod.

We computed several standard fisheries statistics from the data collected on otoliths. These included von Bertalanffy growth equation parameters (see the electronic supplementary material), back-calculated sizes at early ages and total mortality rate (Z, yr^{-1}). To estimate mortality rates, catch curves (Ricker 1975) were constructed for each population. In catch curve analysis, the log-transformed numbers of fish at each age are plotted against age. In modern fisheries, smaller fish are usually not well represented, due to gear bias in capturing them, but larger fish typically display an exponential decline (or linear, when abundances are log-transformed) in numbers at age. The slope of the linear portion of the catch curve is an estimate of total mortality rate, Z. We computed Z for the Neolithic, 1995 and 2003 populations two ways. First, we regressed the log-transformed counts of recruited fish against age; the slope of this line is an estimate of Z (King 1995). Second, we calculated survival (S) using the method of Chapman & Robson (1960). Z may be estimated as approximately $-\ln(S)$, and the variance is $\cong (1 - S^2)/nS$, where n is the number of recruited fish. This method tends to be more robust to stochastic non-sampling error (Dunn *et al.* 2002). Numbers of fish at age for the 1995 and 2003 estimates were obtained from ICES (2007).

3. RESULTS

Size and age means and ranges varied between the three sampled populations (table 1). The span of both lengths and ages was the smallest for the Neolithic sample (29–88 cm). Only four individuals were age 2 years and three more than age 8 years; most (75%) were ages 3–5 years. The age spread was skewed towards younger fish in the 1995 and 2003 samples and included yearlings ($n = 9$) in 1995 and numerous age 2 fish in both modern samples. Maximum age observed in all groups was 10 years. Neolithic fish were significantly larger and older than the modern fish (table 1; figure 2). Fish harvested in 1995 were larger and slightly younger than those captured in 2003. Total lengths and ages were both substantially lower in the stocks compared with the fisheries, since the fisheries target larger fish (table 1; figure 2), although large fish were also caught in the Argos trawls.

Estimated parameters of the von Bertalanffy growth model indicated that the Neolithic cod had a smaller asymptotic length (L_∞) than the modern cod, but grew faster (growth rate parameter K; table S-1 in the electronic supplementary material, figure 3). Asymptotic length was significantly lower in Neolithic versus both 1995 and 2003; Neolithic K-value was significantly higher than that in 1995, but not in 2003 ($p < 0.05$).

The distribution of back-calculated sizes at age differed in the younger age classes (table 2). Neolithic cod were more than 10% larger at age 1 year than either of the

Table 1. Summary statistics of total lengths (TL, cm) and ages (yr) of the Neolithic, 1995 and 2003 populations. Modern data are from ICES areas 25 and 27 (figure 1).

| group	mean TL, cm	s.d.	N	s.e.	lower 95% CI	upper 95% CI
Neolithic	56.4	10.0	520	0.439	55.6	57.3
1995 catch	49.5	11.1	8573	0.120	49.3	49.7
1995 stock	33.4	10.9	21652	0.074	33.3	33.5
2003 catch	48.2	9.9	5888	0.129	48.0	48.4
2003 stock	31.1	9.8	9771	0.099	30.9	31.3
group	mean age, yr	s.d.	N	s.e.	lower 95% CI	upper 95% CI
Neolithic	4.65	1.29	520	0.056	4.54	4.76
1995 catch	3.11	1.16	8573	0.013	3.09	3.13
1995 stock	2.17	0.93	21652	0.006	2.16	2.18
2003 catch	3.57	0.94	5888	0.012	3.55	3.59
2003 stock	2.17	0.91	9771	0.009	2.15	2.19
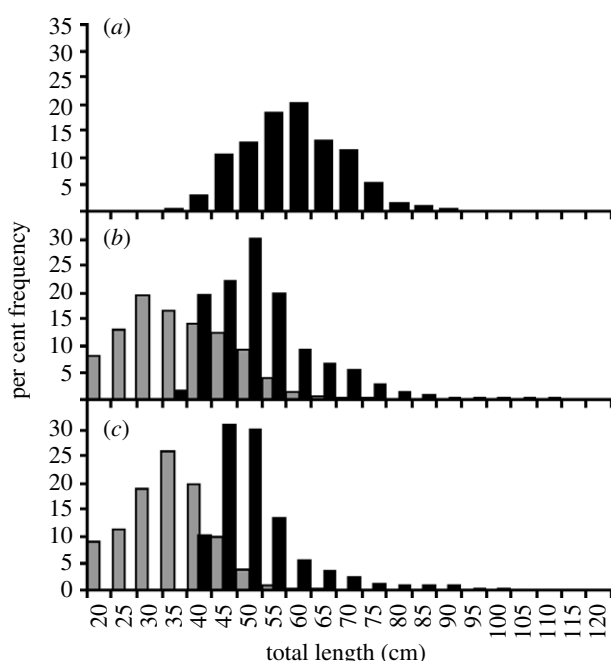
Figure 2. Length frequencies of (*a*) Neolithic and (*b*, *c*) modern (1995 and 2003; ICES areas s.d. 25 and 27) Baltic cod. (*a*) black bar, Neolithic; (*b*) grey bar, 1995 stock; black bar, 1995 fishery; (*c*) grey bar, 2003 stock; black bar, 2003 fishery.

modern groups, and were somewhat larger at age 2 years as well (table 2). By age 3 years, all three groups were statistically indistinguishable.

Estimated total mortality rate, Z_{est}, was the lowest in the Neolithic, highest in the 2003 and intermediate in the 1995 sampled populations (table 3). Results were qualitatively similar among groups, regardless of which calculation method was used (table 3).

Examination of the outermost annuli of the Neolithic otoliths indicated that captures increased monotonically from spring through winter (figure 4), with 10.6% of captures in the spring and 45% in the winter season. This new finding demonstrates that Stone Age fishing was not, as often assumed, restricted to spring–summer spawning periods. Although all age classes showed increased captures in winter, the pattern was strongly driven by age 4, the dominant age class in the otoliths surveyed.

4. DISCUSSION

(a) *Demographics*

Cod remains found at Ajvide represent a long-term fishery. In that fishery, mean lengths and ages were larger than those found in the Baltic Sea in a proximal region in 1995 and 2003. However, Ajvide lengths and ages were smaller than those reported for cod in the open Atlantic in ancient times (Bødker Enghoff 1999; Jackson *et al.* 2001), although such data are sparse. Total mortality estimates were lower in Neolithic times than in either 1995 or 2003, and lower than most of the estimates for fishery-induced mortality in the region from 1966 to 2006 (mean $F_{ages\ 4-7} = 0.943 \pm 0.22$ s.d., range 0.45–1.41; ICES 2007). Zonation on the otolith edges indicated that most Ajvide cod were captured in winter.

Von Bertalanffy growth parameters indicate that Neolithic fish at Ajvide grew to smaller asymptotic lengths, but more quickly, than either of the modern groups examined. This was also substantiated by the fact that Neolithic cod were significantly larger at younger ages (ages 1 and 2 years) than those caught in 1995 and 2003. Whereas the von Bertalanffy parameters of asymptotic length (L_∞) and growth rate (K) tend to be linked (e.g. He & Stewart 2001); in the present case, they do not appear to be tightly so. Rather, adding more large observations (from vertebrae, figure 3) to the Neolithic dataset resulted in increasing L_∞ without substantially altering K.

He & Stewart (2001) provided statistical relationships using von Bertalanffy parameters to estimate age at first reproduction, but lengths at first reproduction are also required; this information is not available for the Neolithic fish. ICES (2007) reports increased frequency of maturity in ages 2, 4, and 5 years of Baltic cod between 1966 and 2006, but a decline in maturity at age 3. Cardinale & Modin (1999) reported declines in both length and age at maturity from the 1980s, when stocks were abundant, to the 1990s when they were overfished. In general, the phenomenon of fishery-induced 'juvenation' (Ottersen 2008) appears to be occurring in the modern Baltic cod, although currently available analyses do not extend as far back as for Arctic cod.

For some cod populations, e.g. Arctic cod, it has been possible to estimate age at first reproduction from otolith growth characteristics (Williams & Bedford 1974). Jørgensen (1990) applied this method to northeast Arctic cod and found that between 1923 and 1976, median age at
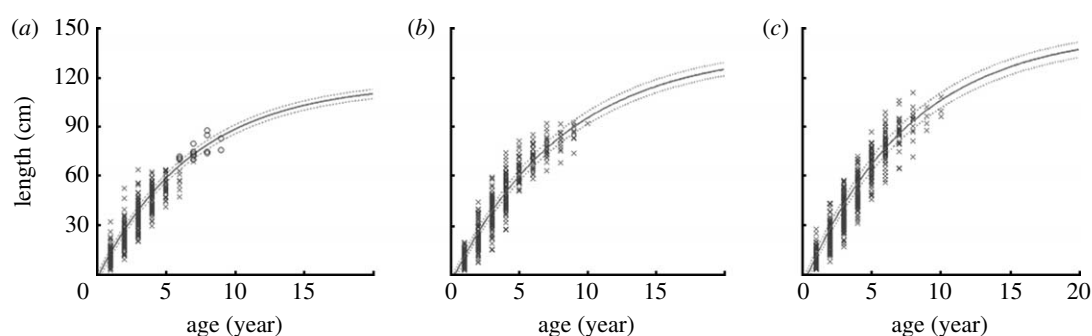
Figure 3. Bayesian estimated von Bertalanffy growth curves fitted from the (*a*) Neolithic, (*b*) 1995 and (*c*) 2003 otolith increment data. Open circles on Neolithic plot indicate measurements made on vertebrae. Cross symbols indicate measurements made on otolith increments.

Table 2. Back-calculated mean lengths (cm) $\pm$s.e. at ages 1 to 3 years for the Neolithic, 1995 and 2003 populations, and tests (ANOVA) of significance. Letter superscripts denote *post hoc* tests (unequal HSD) within a given age class.

length class	Neolithic	1995	2003	F	p	n
all individuals						
$L_{age\ 1}$	10.64 (0.34)[a]	8.70 (0.35)[b]	9.00 (0.31)[b]	9.347	0.0001	484
$L_{age\ 2}$	23.49 (0.54)[a]	21.87 (0.56)[b]	22.57 (0.49)[a,b]	2.857	0.06	476
$L_{age\ 3}$	37.01 (0.67)[a]	37.39 (0.74)[a]	37.55 (0.64)[a]	2.405	0.09	444

Table 3. Estimated total mortality rates (Z_{est}, yr^{-1}) derived from catch-curve analyses, based upon recruitment at age 4.

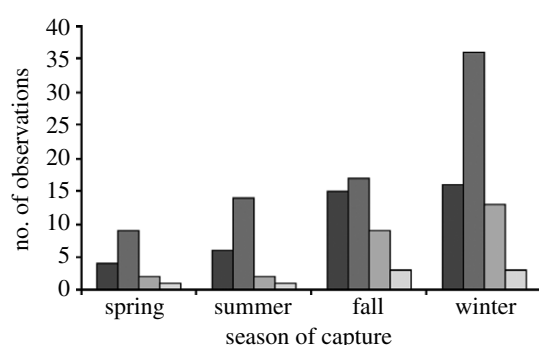|	Neolithic	1995	2003
(a) regression-based estimates			
Z_{est}	0.750	1.033	1.153
s.e.	0.098	0.066	0.066
95% CI	± 0.19	± 0.16	± 0.16
(b) Chapman–Robson estimates			
Z_{est}	0.747	0.990	1.276
s.e.	0.0291	1.05×10^{-5}	1.29×10^{-5}
95% CI	$\pm 1.4 \times 10^{-3}$	$\pm 2.1 \times 10^{-5}$	$\pm 2.5 \times 10^{-5}$

Figure 4. Estimated season of capture of Neolithic fishes partitioned by age class. Black, age 3; dark grey, age 4; light grey, age 5; white, age 6.

maturity fell by approximately 2.5 years. Such analysis has not been attempted for Baltic Sea cod, given the difficulties in reading their otoliths. Newer methods based on the suites of chemical constituents in otoliths (e.g. Campana & Thorrold 2001) may eventually provide 'chemical signatures' of movement to Baltic spawning areas, but such work is as yet only exploratory (K. E. Limburg 2006–2008, unpublished data).

(b) *Potential sources of bias*

There are numerous sources of bias possible in fisheries analyses. For example, different gear types typically target different fish sizes. The gears used in the modern fishery are gillnets and trawlers. These targeted fish larger than 35 cm in 1995 and 38 cm in 2003 (although our otolith samples included smaller fish). The Ajvide fishery consisted of both hook-and-line fishing and nets that were pulled near shore, evidenced by approximately 500 fish hooks, and a number of birch bark net floats and stone sinkers recovered. Fifty-six intact fish hooks ranged from 23 to 78 mm in length, with a mean size of 54.2 mm and breaking strength (Olson *et al.* in press) well in excess of the average Ajvide cod. There are few studies that compare sizes of fishes caught in trawl versus hook-and-line fisheries. However, a study of two cod fisheries (one long line with hooks, the other trawl) in the same area of Georges Bank showed that trawl gear tended to capture a higher proportion of larger fish than long-line gear, although the overall size ranges were essentially identical between the two gears (L. O'Brien & R. Mayo, NOAA Fisheries, Woods Hole, MA 2002–2006, unpublished data). Thus, we tentatively conclude that the Neolithic hook fishery would not have been biased towards capturing larger fish in the coastal zone.

Larger Stone Age fish, such as those captured outside the Baltic in North Atlantic sites, might have not been caught at Ajvide because they broke the fishing lines. However, it is unlikely that larger fish were missed owing to fishing line breakage. Along with evidence from numerous large fishing hooks, it is known that the Neolithic people were able to produce lines that could bear the weight of harpooned seals, so clearly they could make fishing line to bring in struggling cod. Calculations of breaking strength of bast cordage manufactured from *Tilia* sp., used for line by Neolithic cultures (79 N for a 2 mm thick line, based on Myking *et al.* (2005)) suggest that the line would not break when large fish were hooked.

(c) *Why were so few small (and very large) cod found at Ajvide?*

It is striking that the Neolithic otoliths were from cod of constrained size and age ranges. Small, very young cod were sparsely represented. In part, the lack of small cod remains might have been due to differential preservation and recovery of small bones and otoliths, but this seems unlikely as other very small bones have been recovered (e.g. herring bones). Furthermore, smaller cod (mean TL 42.1 ± 9.1 cm, range 25–65 cm) were found at Jettböle, a shallower, more protected site in Åland north of Gotland (Olson & Walther 2007). Thus, either the small cod were not to be found in Ajvide habitats when and where they were fished, or they were rare owing to be targeted by other predators, or some combination of these.

In general, most Baltic cod recovered from the Mesolithic and Neolithic were small (less than 35 cm) to medium sized (45–70 cm; Bødker Enghoff 1994, 1999; Makowieki 2003; Olson & Walther 2007; Olson *et al.* 2007). Cod remains found at Ajvide are considered to be among the larger found within the Baltic Stone Age remains. However, very large cod (greater than 85 cm) may have been rare at Ajvide and other sites because they stayed offshore, beyond convenient reach of fishers.

On the other hand, Baltic cod are genetically highly distinct from populations in the North Sea and Atlantic (Nielsen *et al.* 2001; O'Leary *et al.* 2007), which accounts for their generally smaller size, at least historically (Bødker Enghoff 1999). Thus, an alternative explanation would be that Ajvide cod remains may actually reflect the size ranges present. Currently, there is insufficient evidence to support either explanation definitively. Nevertheless, even lacking such large animals, the evidence is strong that modern Baltic fisheries, which target the largest individuals, exploit smaller cod today than did the Neolithic fishers of 4500 years ago.

5. PERSPECTIVE

There is little doubt today that Baltic cod is overfished and management faces major challenges. Archaeological evidence presents a baseline against which this fishery can be assessed. Reconstructed demographics from a Neolithic population show that cod were on average larger, older, and had lower total mortality than the heavily exploited modern stocks. The Neolithic remains here revealed an exploited population that was not as radically different in size as historic versus modern open Atlantic cod. However, these findings should be tempered by the fact that the Ajvide fishers most likely exploited fish swimming closer to shore, whereas the modern offshore fisheries are able to exploit more and larger fish, if available. Given this, we suggest that the contrast between the Ajvide and modern gillnet and trawl fisheries is conservative; even larger, older fish may have been beyond easy reach of the Neolithic fishers. Finally, further work to assess the differences in age at sexual maturity is needed.

ENDNOTE

[1]Details of the sampling program are described in the 'Technical Report for the Swedish National Programme for Collection of Fisheries Data 2003'.

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